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Published in:
Animal Behavior

DOI:
10.1006/anbe.1996.0099

Publication date:
1996

Anim. Behav., 1996, **51,** 957–966

Post-fledging care, multiple breeding and the costs of reproduction in the great tit

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(Received 22 March 1995; initial acceptance 23 June 1995; final acceptance 4 August 1995; MS. number: 4883)

Abstract. In species that initiate multiple broods in a single season there is usually a trade-off between the number of young in the first brood, and the timing and occurrence of subsequent broods in the same season. The hypothesis that experimental reduction of clutch size reduces the duration of post-fledging care was tested in great tits, *Parus major*, and the effect of second clutches on post-fledging care was also investigated. Parental care continued for 20 days (range 10–32 days) after fledging. Investment in successive clutches overlapped, and the duration of post-fledging care was positively correlated with the inter-clutch interval. Second clutches reduced the female's contribution to post-fledging care. The clutch size manipulation did not affect the duration of post-fledging care. It is concluded that factors other than the duration of post-fledging care mediate the effect of clutch size manipulations on second clutches, and an alternative hypothesis is discussed.

Trade-offs between fitness components are central to the study of the evolution of life histories. In many species, brood (or litter) size manipulations have been used to study such trade-offs (reviewed by Lessells 1991; Roff 1992; Stearns 1992). When broods/litters are enlarged in multiple breeders (species that rear more than one batch of young per season), subsequent broods are delayed and/or fewer are started (Fuchs 1982; Slagsvold 1984; Finke et al. 1987; Hegner & Wingfield 1987; Smith et al. 1987; Tinbergen 1987; Lindén 1988; Tinbergen & Daan 1990; Stouffer 1991; ten Cate & Hilbers 1991; Conrad & Robertson 1992; Møller 1993; Verhulst 1995). How these costs of reproduction arise is not clear. This is unfortunate, because predictions concerning the effect of the costs of reproduction on optimal reproductive strategies may depend on the mechanisms mediating these costs.

In our study of great tits, *Parus major*, breeding on Vlieland (The Netherlands), an experimental reduction in clutch size increased the proportion of pairs that started a second clutch, and decreased the inter-clutch interval (Verhulst 1995), as found in previous studies of this species (Slagsvold 1984; Smith et al. 1987; Tinbergen 1987; Lindén 1988; Tinbergen & Daan 1990). Brood size manipulations also affect the development of the young: growth is enhanced in experimentally reduced broods (Slagsvold 1984; Smith et al. 1987; Tinbergen 1987; Lindén 1988; Tinbergen & Daan 1990; Verhulst 1995). This led Tinbergen (1987) and Smith et al. (1989) to hypothesize that brood size manipulations could affect the period of care required after fledging. This would allow the parents to start the second clutch sooner when clutch size was experimentally reduced. This is important because second clutches are more profitable when started early (Smith et al. 1989), and hence the reduction would result in a larger proportion of birds for which it is profitable to start a second clutch. We studied post-fledging care in great tits, and tested the hypothesis that an experimental reduction of the number of young in the first brood results in shorter post-fledging care.

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Post-fledging Care

Davies (1976, 1978; see also Moreno 1984) concluded that young become independent of their parents when self-feeding is energetically more profitable than begging food from the

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parents. Whether it is more profitable for young to beg from the parents depends not only on food availability and the foraging ability of the young, but also on the willingness of the parents to feed the young. Whether it is profitable for the parents to continue investment in their young will depend, among other things, on the benefits associated with alternative activities. For example, parents may decide to start another clutch within the same season, which could interfere with post-fledging care.

Theoretically, parents should reduce the time invested in a clutch if it is followed by another clutch (Verhulst 1995). This arises because parents pay a price for delaying the second clutch, owing to the seasonal decline in reproductive value of a clutch (Smith et al. 1989). This prediction was confirmed by an experiment with great tits in which second clutches were removed, prolonging post-fledging care (Verhulst 1995). However, investment in successive clutches overlaps in many multiple breeders, which was not considered in the model. In birds, the male usually tends the offspring of the first clutch while the female lays and incubates the new one (Lack 1943; Delius 1963; Haftorn 1978; Edwards 1985; Zaias & Breitwisch 1989; With & Balda 1990). This makes it more complex to predict the effect of second clutches on the duration of post-fledging care. We therefore investigated the effect of second clutches on the participation of males and females in post-fledging care, which has rarely been described in detail, and also investigated the effect of natural variation in the occurrence and timing of second clutches on post-fledging care.

METHODS

Study Area and General Methods

Field work was carried out on Vlieland (Verhulst 1995), an island in the Dutch Waddensea, in 1989–1991. Because of its isolation, family flocks do not leave the study area, as reported for other populations (Drent 1984), which makes Vlieland especially suitable to study post-fledging care. There is one large woodland on Vlieland (the village wood), and four small woodlands (collectively called the west). The woodlands consist mainly of pine (*Pinus* spp., *Picea sitchensis*), with patches of oak, *Quercus robur*.

We checked all nestboxes at least once a week during the breeding season and recorded laying date (taken to be the date the first egg was laid) and clutch size. We checked nests daily around the expected day of hatching to establish the hatching date. Adults were captured in the nestbox with spring traps when the young were 8–10 days old. We ringed the young when they were 15 days old (day of hatching = 0), and at the same time measured mass, tarsus and wing length. In addition to numbered aluminium rings, the young were colour-ringed so that those from control and experimentally reduced broods could be recognized from a distance in 1989, and so that individual broods could be recognized in 1990 and 1991.

We visited broods daily after 1500 hours Central European Time (CET) from day 16 after hatching onwards to establish fledging date. We counted the young without handling them to minimize the risk of premature fledging. Great tit broods typically fledge in the morning (Lemel 1989; Verhulst 1995), so the day of fledging can be established by checking the nests in the late afternoon. As a rule, all young of a brood fledged on the same day.

When we discovered them in time, we visited second clutches daily during laying to establish the date on which the female started incubation. To measure the time that females incubating the second clutch had available to care for first-brood fledglings we observed four nestboxes with second clutches in the incubation stage. Each nestbox was observed for 2 h from 0900 to 1700 hours CET on 2 separate days with a telescope from as far away as the vegetation permitted (usually more than 50 m). During the observations we recorded the time that the female entered and left the nestbox and from these data calculated the proportion of time the female spent in the nestbox.

Experiments

Clutch size manipulations

We selected 114 dyads of first clutches (44 in 1989, 30 in 1990, 40 in 1991) matched for laying date (maximum difference of 2 days) and clutch size (maximum difference of one egg). Taking laying date, clutch size and distribution of the clutches over the different woods into account, we manipulated one randomly chosen clutch in each dyad. We replaced 50% of the eggs by plastic eggs,

approximately 6 days after the last egg was laid. There were no clutch enlargements. Prior to replacing an egg we observed the nestbox from a distance until the female was seen to leave it. We then replaced the eggs as fast as possible to avoid detection by the breeding pair. The artificial eggs were removed from the nest with the same procedure 1 day after the eggs hatched.

Removal of second clutches

In addition to the clutch size manipulations, in 1990 and 1991 we removed the second clutches of some pairs shortly before hatching to investigate the costs of rearing a second clutch (Verhulst 1995). We selected dyads of second clutches with approximately equal laying date and clutch size. Within each dyad, first clutches experienced the same treatment (control or reduced). Taking laying date and clutch size into account, we removed one randomly chosen clutch in each dyad shortly before hatching, circa 9 days after clutch initiation.

In 1990 many pairs were still caring for the first-brood fledglings when the second clutch was removed, but in 1991 all pairs, except one, had stopped post-fledging care at the time the second clutch was removed. In this paper the pairs from which the second clutch was removed in 1990, as well as the one pair in 1991 that was still caring for its first-brood young when the second clutch was removed, were excluded from the analysis of the duration of post-fledging care.

Post-fledging Care

We studied post-fledging care in a subsample of all pairs involved in the clutch size manipulation, because this work was carried out only in the village. We divided the village wood into 15 smaller areas, and searched each area once every 2 days. We searched for family flocks on foot, and usually heard them before they were seen. When the family was found we identified them by their unique combination of colour rings. We recorded time and place of observation and presence of the parents. Post-fledging care was considered to be still continuing when young were fed by the parents or seen begging towards the parents. Deciding whether post-fledging care was still continuing was not difficult because begging and/or feeding was observed in practically all instances where parents and young were seen in the same location. Observations of individual families were terminated when we were convinced that all members of the family flock had been identified, or when the family had disappeared from sight.

Although each part of the study area was searched only once every 2 days, this does not imply that the resolution of our data on the duration of post-fledging care is 2 days. The different areas bordered on each other, and when searching a certain area, we often heard family flocks in neighbouring areas. Family flocks were identified regardless of the place where they were found. In addition, family flocks tended to roam around in the course of a day, and could be encountered in different areas on a given day.

Data Analysis

To evaluate the effect of second clutches on the participation of males and females in post-fledging care we grouped the observations by reproductive stage: pre-laying (from fledging until the first egg of the second clutch was laid), laying, incubation (laying and incubation usually overlapped, and the days of overlap were included in the incubation stage). Eleven second clutches were removed during the incubation stage and the period before and after clutch removal were treated separately. For control pairs of the removal experiment the day that the clutch of the experimental pair in the dyad was removed was taken as the boundary. The participation in post-fledging care was taken to be the proportion of observations of a family flock where a parent was present.

In addition we defined time intervals that were comparable with the reproductive stages described above. We calculated for each year of study the average number of days after fledging that (1) laying of the second clutch started, (2) incubation started and (3) the clutch removal took place. Using these figures, we calculated the participation of males and females in post-fledging care for pairs that did not start a second clutch for time intervals that could be compared with pairs that did start a second clutch.

We analysed the data with multiple regression with a normal error distribution and with logistic regression, using year, experiments and the presence of a second clutch as categorical variables. In the logistic regression analyses *P*-values were

Table I. Observation frequency and duration of post-fledging care (PFC) for control and experimental clutches in the different years of study

	Control			Reduced		
	$\bar{X}$	SD	*N*	$\bar{X}$	SD	*N*
1989						
Proportion broods seen	0.86	—	23	0.82	—	22
Observation frequency	0.25	0.16	20	0.26	0.16	18
Duration PFC, all data	18.4	7.4	20	16.9	5.4	18
Duration PFC*	19.9	6.0	18	17.6	4.7	17
1990						
Proportion broods seen	1.0	—	11	0.75	—	12
Observation frequency	0.32	0.14	11	0.26	0.14	8
Duration PFC, all data	18.2	3.9	11	16.7	7.7	9
Duration PFC*	18.2	3.9	8	18.8	4.9	8
1991						
Proportion broods seen	0.73	—	15	0.89	—	18
Observation frequency	0.19	0.11	10	0.25	0.13	15
Duration PFC, all data	12.6	7.1	11	13.3	7.7	16
Duration PFC*	15.2	4.4	9	15.0	6.5	14

Observation frequency is the proportion of days that the family was observed between fledging (including the day of fledging) and the day of the last observation (excluding the last observation).
*Omitting pairs where PFC was less than 7 days.

computed using the chi-squared test when the deviance was smaller than the degrees of freedom, and the *F*-test when the deviance was larger than the degrees of freedom. Thus *P*-values are conservative. All statistical tests are two-tailed.

RESULTS

Transition to Independence

We observed independent young before the last observation of the family flock in 13% of all cases ($N=39$, 1990 and 1991 pooled; 1 ($N=1$), 2 ($N=3$) or 3 days ($N=1$) before the last observation), and these young were not subsequently seen again in the family flock. In addition, in four cases independent young were first observed on the day of the last observation of the family flock. Since the different young of a brood reached independence within a relatively short time span, the brood is the appropriate level to analyse variation in the duration of post-fledging care.

Observation Probability

The estimated duration of post-fledging care depends not only on the duration of flocking but also on the probability that we would observe that flock; if the observation probability is relatively high, the estimated duration of post-fledging care will be relatively long. Therefore we evaluated the effect of the clutch size manipulation on the observation probability.

When years were pooled ($\chi^2=0.2$, $df=2$, $P=0.9$), the proportion of families seen at least once after fledging did not differ significantly between the control and experimental categories (Table I; control: $\bar{X}=0.86$, $N=49$; experimentally reduced clutch: $\bar{X}=0.83$, $N=52$; $\chi^2=0.2$, $df=1$, $P=0.7$). We calculated the observation frequency for families seen at least once. This was defined as the proportion of days that the family was observed between fledging (including the day of fledging) and the day of the last observation (excluding the last observation). Three broods that were observed on the day of fledging only were excluded from this calculation. Controlling for year (logistic regression: $F_{2,79}=1.2$, $P=0.3$), the clutch size manipulation had no effect on the observation frequency ($F_{1,78}=0.2$, $P=0.7$; Table I). When years and experimental categories were pooled, the mean probability of observation per day was 0.26 (SD = 0.14, $N=82$). The observation frequency increased significantly during the 15

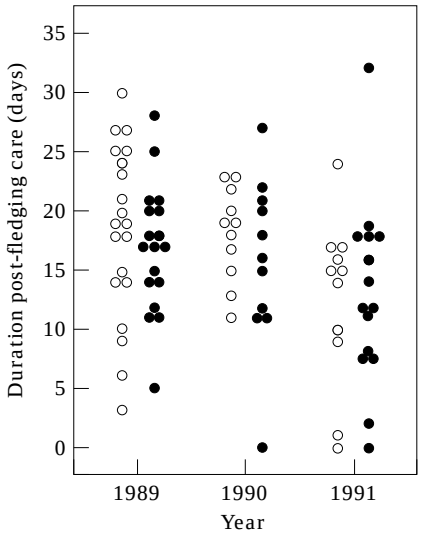

Figure 1. Duration of post-fledging care of control (○) and experimental (●) pairs, in the 3 years of study.

days before the last observation (logistic regression, controlling for year and family, $F_{1,1007}=5.0$, $P<0.03$). This increases the precision of our estimates of the duration of post-fledging care.

Duration of Post-fledging Care

Post-fledging care lasted on average 16.1 days (SD = 6.9, $N=85$), but was variable (Fig. 1). However, in some broods all young may have died before they reached independence. Furthermore, because the observation probability was less than 1, only minimum estimates of the duration of post-fledging care can be made. We first evaluate the effect of these factors on our observations.

Mortality before independence

Pairs where post-fledging care lasted less than 7 days ($N=8$) produced no recruits (fledglings recaptured as breeding birds), while 55% of the remaining pairs ($N=77$) produced one or more recruits each. In 1990 and 1991 independent fledglings could be identified from their colour rings: none was observed from broods where post-fledging care lasted less than 7 days ($N=5$), while independent young were seen from 93% of the remaining broods ($N=48$). This strongly suggests that observations of a short period of post-fledging care can be attributed to fledgling mortality before independence was reached. Therefore all pairs where the duration of post-fledging care was shorter than 7 days have been omitted from the analyses. This did not change any of the results.

Underestimation of the duration of post-fledging care

Among all pairs for which independent young were observed, post-fledging care lasted 16.3 days (SD = 5.2, $N=39$; using data from 1990 and 1991). When all pairs where the interval between the last observation of the intact family flock and the first observation of independent fledglings was more than 2 days were omitted from the data set, post-fledging care among the remaining pairs lasted 19.1 days (SD = 5.1, $N=16$). This suggests that we underestimated the duration of post-fledging care by approximately 3 days.

The observation probability can also be used to estimate the time by which the duration of post-fledging care was underestimated. The observation probability was 0.33 on the last 6 days of post-fledging care, which implies that on average a family flock was observed every third day. This suggests that the duration of post-fledging care was underestimated by 2 days, which is very close to the previous estimate (3 days), based on a selection of pairs where young were observed shortly after independence.

Unmanipulated pairs

When years were pooled, the observation duration of post-fledging care in control pairs was 18.3 days (SD = 5.3, $N=38$). Thus, when corrected for the underestimation, on average post-fledging care in control pairs lasted 20–21 days. The shortest period of post-fledging care of a pair that resulted in independent young was 10 days, and the longest observed period of post-fledging care was 32 days.

The duration of post-fledging care varied significantly between years (Fig. 1; $P<0.04$). Post-fledging care was approximately 4 days shorter in 1991 than in the other two years (Table I).

Clutch size manipulation and post-fledging care

Controlling for year, there was no significant effect of the clutch size manipulation on the

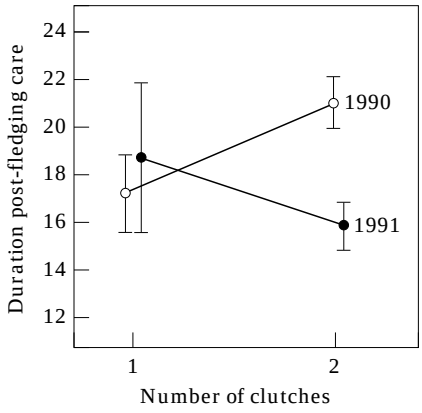

Figure 2. Duration of post-fledging care ($\bar{X} \pm$ SE) for pairs with or without a second clutch in 1990 (○) and 1991 (●). Pairs where post-fledging care was shorter than 7 days were omitted from the calculation.

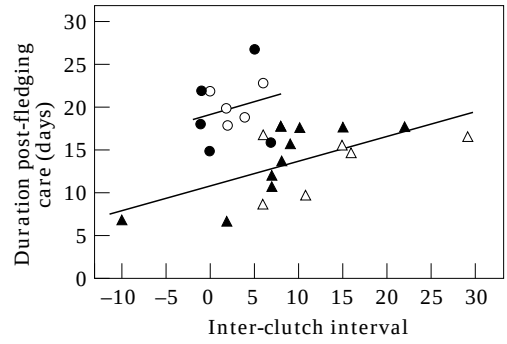

Figure 3. Duration of post-fledging care and inter-clutch interval for pairs with a control clutch (○, △) or an experimentally reduced first clutch (●, ▲) in 1990 (○, ●) and 1991 (△, ▲).

duration of post-fledging care (Table I; experimental effect: $\bar{X} \pm$ SE = 1.0 ± 1.2 days, $F_{1,73} = 0.7$, $N = 77$, $P = 0.4$), and there was no significant interaction between year and the clutch size manipulation ($F_{2,71} = 0.6$, $P = 0.6$). Controlling for year, analysis of the effect of variation in number ($P > 0.5$) and quality (mass, tarsus or wing length) of fledglings (all $P > 0.3$), the date of hatching or fledging (both $P = 0.2$) also failed to produce significant results (control and experimental clutches pooled).

The absence of a significant effect of the clutch size manipulation on the duration of post-fledging care could be due to the power of the test applied. Following Zar (1984), we calculated that, given our sample sizes and standard deviation, a true difference between experimental categories of 3.9 days would have yielded a significant result at the 5% level (two-tailed) in 90% of cases. Thus it is reasonable to conclude that if there is an (undetected) effect of the experiment on the duration of post-fledging care, such an effect is likely to be less than 3.9 days.

Post-fledging Care and the Second Clutch

We evaluated if presence of a second clutch affected the duration or quality of post-fledging care of first-brood fledglings. In the first year of this study (1989), the proportion of pairs that laid a second clutch was extremely low (11%), and therefore we analysed only the data collected in 1990 and 1991, in which years 58% and 70% of pairs laid a second clutch, respectively.

Duration of post-fledging care

In 1990, post-fledging care was longer when pairs laid a second clutch (difference: $\bar{X} \pm$ SE = 3.8 ± 1.8 days, $P = 0.05$), but in 1991 it was shorter in pairs that laid a second clutch (difference: 3.8 ± 2.5 days, $P = 0.1$). The interaction between year and the presence of a second clutch was significant (Fig. 2; $F_{1,38} = 5.7$, $P < 0.025$), which implies that the effect of a second clutch on the duration of post-fledging care varied significantly between years.

Among pairs with a second clutch, parents may have adjusted the inter-clutch interval to the amount of post-fledging care that the first brood required. Therefore we investigated the relationship between the duration of post-fledging care and the inter-clutch interval in a multiple regression analysis. The inter-clutch interval was taken to be the difference (in days) between the date of fledging of the first brood and the laying date of the first egg of the second clutch. Negative values indicate that the first eggs of the second clutch were laid while the first brood young were still in the nest. One female that started a second clutch with a different male was excluded from this analysis. Controlling for year ($F_{1,23} = 30.8$, $P < 0.001$), the duration of post-fledging care was positively correlated with the inter-clutch interval (Fig. 3; $F_{1,23} = 10.2$, $r^2 = 0.58$, $N = 26$, $P < 0.005$).

There was no significant interaction between year and inter-clutch interval. The manipulation of the first clutch, when added to this model, did not explain a significant part of the variance ($F_{1,22}=0.4$, $P=0.5$).

Participation of males and females in post-fledging care

Using logistic regression we investigated the participation of males and females in post-fledging care at different stages of the second clutch, and compared them with pairs without a second clutch. Observations per family were pooled per reproductive stage, and in this way each family was used as one degree of freedom per reproductive stage in the tests (see Fig. 4 for sample sizes). The participation of the male was reduced at all reproductive stages in the absence of a second clutch (Fig. 4a). This difference was significant at all reproductive stages except during laying of the second clutch (before laying: $\chi^2=4.8$, $df=1$, $P<0.03$; during laying: $\chi^2=2.4$, $df=1$, $P>0.1$; incubation: $\chi^2=27.3$, $df=1$, $P<0.001$; after clutch removal: $\chi^2=12.6$, $df=1$, $P<0.001$). The removal of the second clutch did not have a significant effect on the participation of the male in post-fledging care ($F_{1,21}=1.75$, $P=0.2$).

Participation of the female in post-fledging care before and during laying was not affected by the second clutch (Fig. 4b; before laying: $\chi^2=0.33$, $df=1$, $P>0.5$; during laying $F_{1,45}=0.44$, $P>0.5$). Female participation in post-fledging care was significantly reduced by a second clutch during incubation ($F_{1,45}=23.1$, $P<0.001$) and in the period after manipulation (using only control pairs with respect to the manipulation of the second clutch: $\chi^2=19.5$, $df=1$, $P<0.001$). After manipulation, females from which the second clutch was removed participated more in post-fledging care than during incubation ($\chi^2=15.8$, $df=1$, $P<0.01$) and more than control females ($\chi^2=12.7$, $df=1$, $P<0.01$) at the same time.

Females incubating a second clutch spent 69% of their time on the nest during daylight (SD = 2.4%, $N=4$ females). In 22% of family flock observations at the incubation stage, females were seen to participate in post-fledging care. This implies that females spent most of their time off the nest in the family flock. Females were frequently seen to feed the first-brood fledglings during these observations.

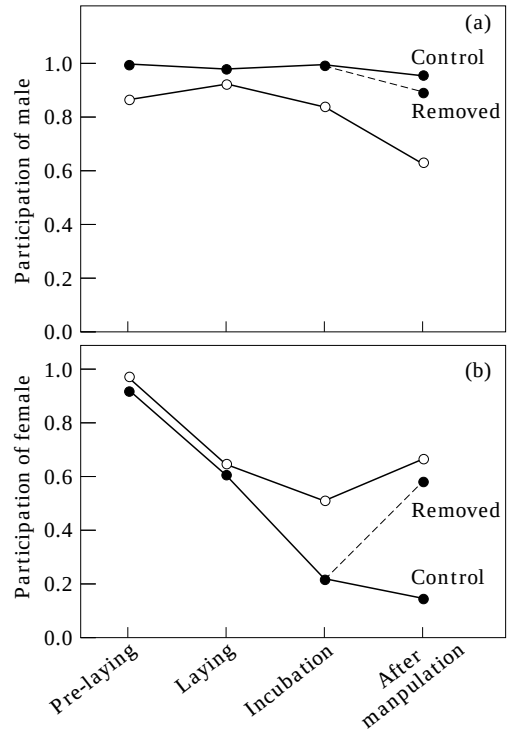

Figure 4. Participation of (a) males and (b) females in post-fledging care of the first-brood fledglings for birds with (●) or without (○) a second clutch (1990 and 1991 combined). Participation was taken to be the proportion of observations of a family flock where a parent was present. Sample sizes (number of families) for both sexes for the successive reproductive stages: with second clutch: 22, 28, 27; control: 12; removed: 11; without second clutch: 15, 21, 20, 9.

During the incubation stage of the second clutch, male parents were observed to perform post-fledging care more frequently in pairs that had laid second clutches (Fig. 4a), while the opposite was true for female parents (Fig. 4b). These effects did not cancel each other out and post-fledging care was significantly reduced in pairs with second clutches during the incubation stage of the second clutch ($\chi^2=4.04$, $df=1$, $P<0.05$).

DISCUSSION

Post-fledging care lasted on average 20–21 days, which is in reasonable agreement with previous

studies (de Goede 1982; Riddington 1992). For the unmanipulated pairs in our study, this brings the total time invested in the first clutch (from laying the first egg until the end of post-fledging care) to 61 days. The duration of post-fledging care varied significantly between years. Several studies have shown an effect of food availability on the duration of post-fledging care (Norton-Griffiths 1969; Higuchi & Momose 1981; Byle 1990), which suggests annual variation in food availability might explain this result. Indeed, preliminary analysis shows that food availability (caterpillar abundance on oaks) during the period of post-fledging care was higher in 1991, when the duration of post-fledging care was short, than in the other two years (unpublished data).

Second Clutches and Post-fledging Care

When pairs laid a second clutch, this had a negative effect on the female's contribution to post-fledging care after the start of incubation (Fig. 4b). This was experimentally confirmed with the removal of second clutches, which increased the time that females spent with the first brood. To our knowledge, this is the first experimental demonstration that care for the second clutch is traded off against care for offspring of the previous clutch. It is likely that the proportion of food that the parents could allocate to the young was also reduced during laying and incubation of the second clutch. We therefore conclude that the second clutch had an adverse effect on the quality of post-fledging care of the first-brood fledglings, which suggests a second clutch will have a negative effect on the reproductive value of the first clutch.

The duration of post-fledging care increased with the interval between the first and the second clutch (Fig. 3). Experimental removal of the second clutch prolonged post-fledging care (Verhulst 1995), which indicates this correlation was at least partly caused by a direct effect of the second clutch on the termination of post-fledging care. However, it can be expected that as a consequence the tits will adjust the inter-clutch interval to the parental care required by the young of the first brood. When broods are small and young are better developed inter-clutch intervals are typically short (e.g. Verboven & Verhulst, in press), in agreement with this possibility.

Clutch Size and Post-fledging Care

When the clutch size of great tits is experimentally reduced a higher proportion of pairs start a second clutch and the inter-clutch interval decreases (Smith et al. 1987; Tinbergen 1987; Lindén 1988; Tinbergen & Daan 1990; Verhulst 1995). We previously tested the hypothesis that this experimental effect on second clutches was mediated by an effect on work rate during rearing of the first brood. However, daily energy expenditure of parents rearing the first clutch did not correlate with the occurrence of second clutches (Verhulst 1995), and this suggests that the trade-off is not a direct consequence of work rate during rearing of the first brood. Therefore we tested the hypothesis that pairs with an experimentally reduced brood cared for their offspring for a shorter period after fledging, because this could explain why clutch size manipulation affected timing and occurrence of second clutches (see Introduction). To our knowledge, this is the first large-scale study in which the effect of clutch size manipulation on post-fledging care has been investigated.

Post-fledging care lasted approximately 1 day less when clutch size was experimentally reduced, but this effect was not significant. Furthermore, variation in number and quality of fledglings was not significantly correlated with the duration of post-fledging care. We therefore conclude that the experimental reduction in clutch size did not affect the duration of post-fledging care. Young in experimentally reduced clutches developed at a higher rate in the nest, and also fledged at an earlier age (Verhulst 1995). We therefore expected that young from experimental clutches would also reach independence sooner after fledging, and the absence of this effect calls for an explanation.

Experimental reduction in the number of young resulted in a larger proportion of pairs that started a second clutch, and a second clutch had a negative effect on the quality of post-fledging care (Fig. 4). The tits may have compensated for this by prolonging post-fledging care. Thus there are possibly two opposing effects of the clutch size reduction on the duration of post-fledging care, and as a result, a clutch size reduction is not predicted to affect the duration of post-fledging care overall (see Fig. 5 for a schematic summary). The fact that the difference between experimental

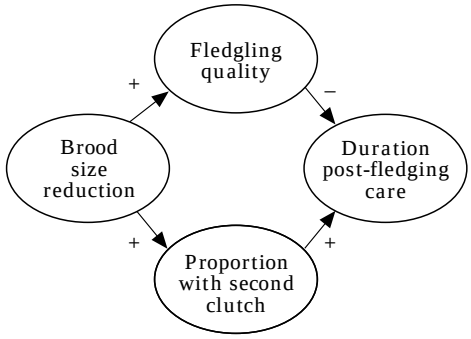

Figure 5. Schematic summary of hypothesized effects of manipulation of the number of young in the first brood on the duration of post-fledging care via different causal pathways.

and control pairs was largest in 1989 (Table I), a year with a low incidence of second clutches, lends some plausibility to this view.

Post-fledging Care and the Costs of Reproduction

Experimental reduction in clutch size did not significantly affect the duration of post-fledging care, but this does not imply that post-fledging care does not play a role in the mechanisms mediating the effect of brood size manipulation on second clutches. Here we discuss another way in which post-fledging care could play a role in an explanation of the experimental effect on the second clutches. Central in this alternative hypothesis is the trade-off between successive reproductive attempts: starting a second clutch reduces the reproductive value of the first clutch, because of the effect of second clutches on post-fledging care (Fig. 4; Verhulst 1995). The effect of this trade-off could be smaller for fledglings from reduced broods, because there are fewer young, which are better developed. Thus according to this hypothesis, pairs with an experimentally reduced brood were able to start second clutches more often because their young suffered less from a reduction in the quality of post-fledging care.

In conclusion, we found no support for the hypothesis that an effect of brood size on the duration of post-fledging care mediates the effect of brood size on timing and occurrence of second clutches (as suggested by Tinbergen 1987; Smith et al. 1989). However, the effect of the second clutch on the reproductive value of the first clutch may depend on the number of young in the first clutch, in which case post-fledging care may still be involved in the mechanism mediating this cost of reproduction. Further experiments are required to test this hypothesis.

ACKNOWLEDGMENTS

Christiaan Both, Andries Datema, Margriet Dijkstra, Eveline Groenewoud, Karen Krijgsveld, Karel Scheepstra, René van der Wal, Huibert van Eck, Klaas van Maanen, Maarten van Steenis, Nanette Verboven and Hans Westendorp participated in the field work, and comments from Daniel Cristol, Serge Daan, Mats Lindén, Juan Moreno and Joost Tinbergen improved the manuscript. Dick Visser prepared the figures. Field work was supported by BION grant 436.911-P to Joost Tinbergen and Serge Daan.

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